CORM MORPHOLOGY IN *HESPERANTHA* (IRIDACEAE, IXIOIDEAE) AND A PROPOSED INFRAGENERIC TAXONOMY[1]

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ABSTRACT

The corm tunics of species of *Hesperantha* vary to a remarkable extent in this African genus in which other morphological characteristics provide little information for classification above the species level. The presumed basic corm type is globose and distinctly asymmetric and has concentric tunics. Globose corms with imbricate tunics, distinctly notched below are believed to be derived while the most specialized are flat-sided and triangular to campanulate in outline, with imbricate tunics, either more or less unbroken below, or notched into segments and often spiny or toothed below. This variation appears to form a coherent pattern and is emphasized in an infrageneric classification in which other taxonomically useful characters are taken into account. Four sections are recognized. Species with concentric corm tunics are assigned to section *Concentrica*; those with globose corms and imbricate tunics are assigned mostly to section *Imbricata*; while most of those with symmetric, campanulate to triangular, flat sided corms with imbricate tunics are assigned to section *Hesperantha*. A distinctive group with bracts having margins partly united around the stem, and either globose or campanulate corms with imbricate tunics are assigned to section *Radiata*. A brief survey of the distribution and distinctive species of each section is outlined following the formal taxonomic descriptions.

INTRODUCTION

Hesperantha is a genus of some 55 species of Iridaceae, Ixioideae, distributed widely in sub-Saharan Africa. The genus consists of small to medium-sized corm-bearing plants, often with white, or pale-colored flowers and a characteristic stigma that divides into three long branches at the mouth of a relatively long perianth tube. Species are concentrated in the winter rainfall region of southern Africa, where some 34 species occur in the southwestern Cape, the adjacent western Karoo and Namaqualand. There is a secondary center in the higher mountains of eastern southern Africa, especially the Drakensberg of Natal and Lesotho. The number of species falls sharply northward through the Transvaal and Zimbabwe with only one species extending into the mountains of East Africa, Ethiopia and Cameroon. *Hesperantha* is currently being studied by O. M. Hilliard & B. L. Burtt (1979:302–304, and in prep.) in the eastern part of its range in the Drakensberg of Southern Africa, and by myself in the Cape winter rainfall area.

A cormous rootstock is a characteristic feature of several monocot families particularly those of Liliaceous affinities, notably Tecophilaeaceae, Colchicaceae, and Iridaceae (Dahlgren & Clifford, 1982). In Iridaceae two different corm types occur (Goldblatt, 1976:670; de Vos, 1977), one in Iridoideae and the other in Ixioideae, to which *Hesperantha* belongs. In Ixioideae variation in corm morphology is considerable, involving shape, size, number of nodes and nature of

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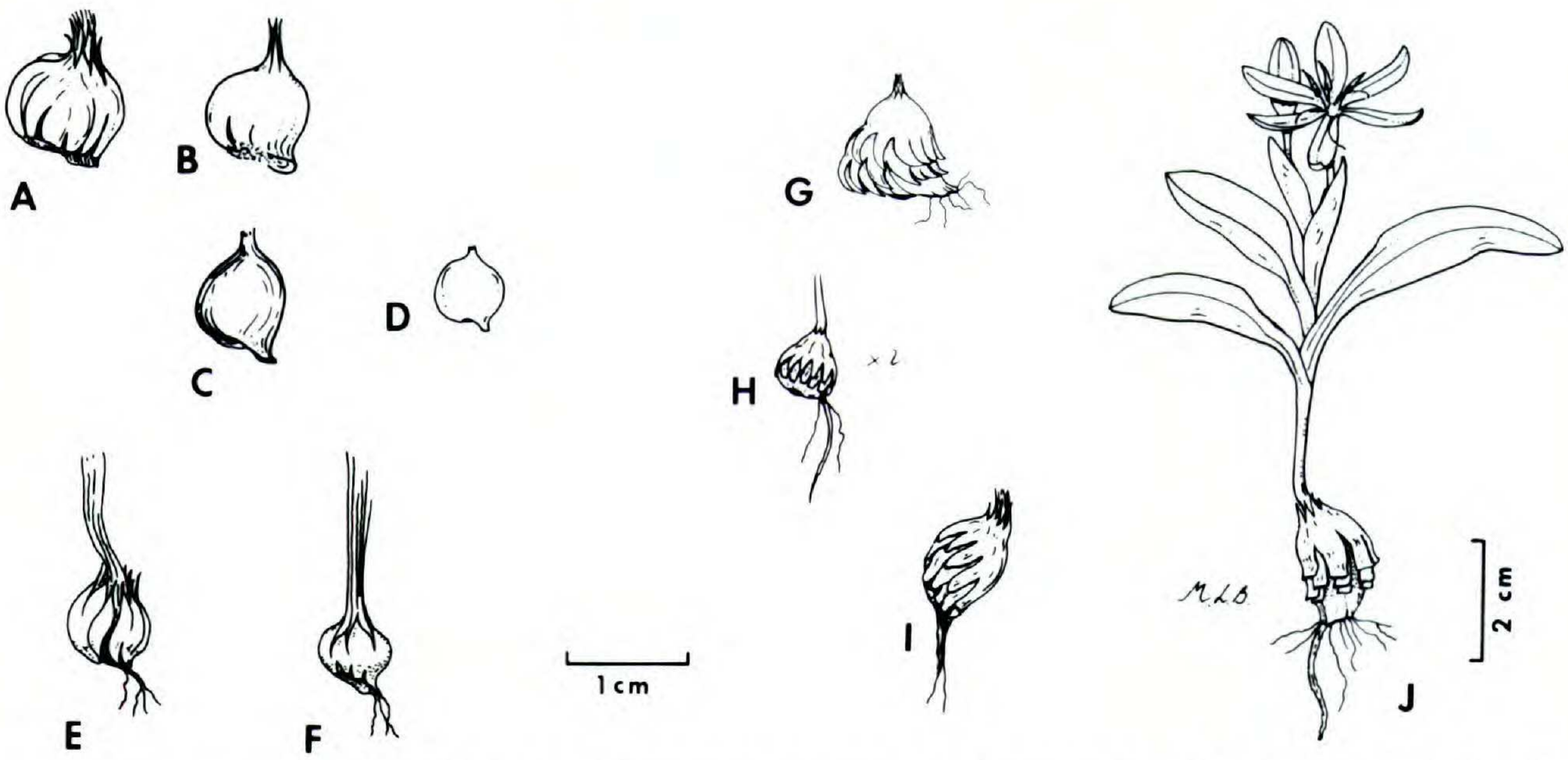

FIGURE 1. Corm morphology of *Hesperantha* sections *Concentrica* (A–F) and *Imbricata* (G–J): A–D. *H. pilosa* with tunic layers progressively removed and the naked corm (D); E. *H. rivulicola*; F. *H. fibrosa*; G. *H. vaginata*; H. *H. bachmannii*; I. *H. pallescens* (bulbils removed); J. *H. humilis* (all more or less life size except J, ×0.5).

the covering layers, which are called tunics. The tunics are derived from specialized cataphylls or the lower parts of the basally sheathing cataphylls or produced leaves and they may be considerably modified and elaborated in some genera. They vary from coarsely to finely fibrous and reticulate to thick and woody in texture. A general discussion of the corms found in Iridaceae is given by Lewis (1954).

In *Hesperantha* corm morphology varies to a remarkable extent within the genus, particularly in the species of the winter rainfall area of southern Africa and this has until now been inadequately documented. The morphology of the corm and corm tunics is described in detail below, followed by a discussion of other important morphological characters. A classification in which corm characteristics are emphasized is presented in the taxonomic part of the paper. My knowledge of the species of eastern southern Africa is limited so that the scheme is based largely on the winter rainfall area species. I hope nevertheless that the classification will prove applicable to the entire genus. A preliminary examination of species outside the winter rainfall area suggests that they can be accommodated in the classification outlined below, although creation of further sections may prove necessary.

CORM MORPHOLOGY

The morphology of the living tissue of the corm of all species of *Hesperantha* is similar except for slight variation in size and shape. The corm is fundamentally asymmetric. Although globose to depressed-globose in general shape, a small projecting ridge is always present at one end of the corm (Fig. 1D, Fig. 2F) and it is from this point only that the roots are produced.

The corm is always covered by specialized layers of tunics and in *Hesperantha* these are usually woody in texture and a single layer is produced annually. The

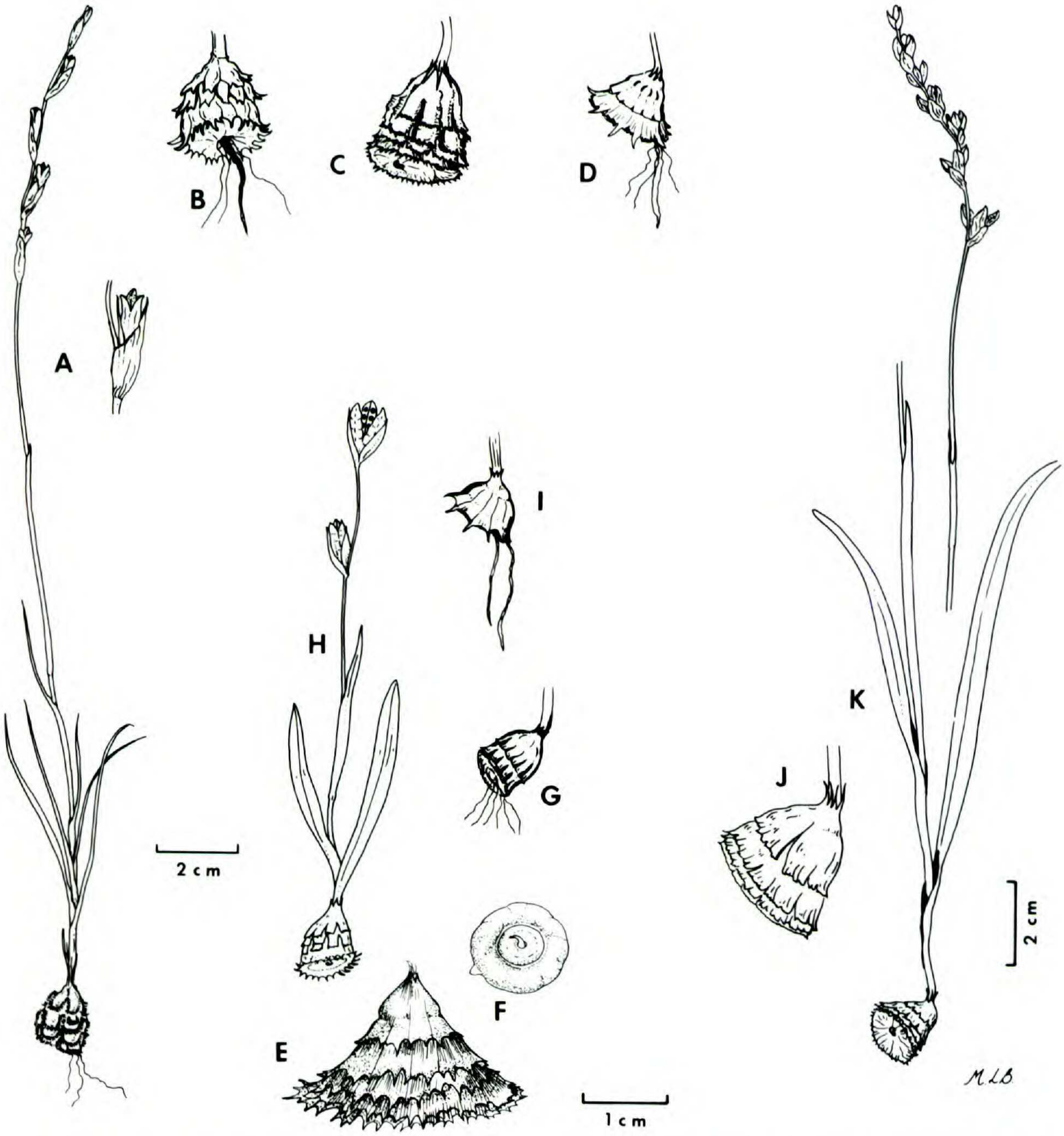

FIGURE 2. Corm morphology of *Hesperantha* sections *Radiata* (A–D) and *Hesperantha* (E–J): A. *H. radiata*, with part of spike enlarged to show sheathing bract; B. *H. radiata*; C. *H. muirii*; D. *H. marlothii*; E. *H. falcata*; F. *H. falcata*, naked corm with tunics removed; G. *H. falcata*; H. *H. cedarmontana*; I. *H. luticola*; J–K. *H. spicata* (all more or less life size except A, H and K, ×0.5).

appearance of the tunics and the way in which they accumulate seems to be the single most taxonomically useful character in the genus above the species level.

The simplest tunic type, and possibly the ancestral condition, since it is also found in species of the related genus *Geissorhiza* (Foster, 1941), is one in which the corm tunics are arranged in concentric layers (Fig. 1A, E, F). In this type the corms are usually more or less globose, with one side flattened below and the flat part extending downward for a short distance. This asymmetry reflects the internal morphology. The tunic layers are usually firm and brittle, but occasionally, especially in high mountain species (e.g. *H. montigena* Goldbl. ined.) they may be papery. Newly formed tunic layers are enclosed by the outer ones

and as successive layers accumulate, the older, outermost ones fragment vertically above and below into regular or more or less irregular-sized pieces (Fig. 1A, E, F). Concentric corm tunics are found in many species that extend throughout the range of the genus and grow in a variety of habitats from moist, well watered situations to arid sites.

A second corm type has imbricate tunics and this is presumed to be the derived condition. Here, the outer layers are displaced upward as new tunic layers are produced annually. The outer layers are typically notched below at regular intervals so that that the lower part of each layer is divided into even-sized segments. The mid-to-upper portion remains unbroken but may become shallowly notched above (Fig. 1G–J, Fig. 2).

Species with tunics of this type may either have globose but asymmetric corms (Fig. 1G, H, I) with one side flattened below and produced downward, or symmetric corms, triangular to campanulate in outline (Fig. 2) with one side completely flat. This type of corm is usually called flat-based although in the ground the flat side is oriented vertically or inclined, and is only basal (i.e. horizontal) in plants growing in shallow soil over rock.

In plants with imbricate corms, the lower margins of the tunic layers may be somewhat fringed (e.g. *H. radiata* (Jacq.) Ker, *H. muirii* (L. Bol.) Lewis; Fig. 2A, C), toothed (e.g. *H. radiata*, *H. falcata* (L. f.) Ker; Fig. 2B, E) or even long-spined (e.g. *H. marlothii* Foster, *H. luticola* Goldbl. ined.; Fig. 2D, I), particularly in species with symmetric, flat-sided corms. In some species with flat-sided corms the outer layers do not split into segments but remain almost entire or lightly fringed to toothed, notably in *H. spicata* (Burm. f.) N.E. Br. (Fig. 2J, K).

Some variation is evident in a few species, notably *Hesperantha radiata* (Fig. 2A, B), in which the tunic margins may be lightly fringed to toothed. In *H. falcata* the corms range from triangular to campanulate in outline (Fig. 2E, G) and the lower tunic margins may be unbroken or variously serrate to toothed.

The distribution of various corm types follows a coherent pattern. Obviously allied species have similar corms, and apparently distantly related species usually have different corms. In this light it has seemed reasonable to regard corm morphology as a very reliable indication of taxonomic relationship. An infrageneric taxonomy in which the corm characteristics are strongly emphasized is proposed in the second part of this paper.

Other Morphological Characteristics

Habit, Leaf and Stem

Most species of *Hesperantha* are small to moderate-sized herbs with simple to few branched, aerial stems. One modification that stands out is suppression of the stem and consequent acaulescent habit. Accompanying the stem reduction are flowers with long perianth tubes and large, leaf like floral bracts. This habit occurs in *Hesperantha latifolia* (Klatt) de Vos, a Namaqualand species; in four western Karoo species, *H. humilis* Baker, *H. flava* Lewis and *H. hantamensis* Schltr. ex Foster, and the apparently unrelated *H. luticola*; as well as in the Drakensberg species *H. crocopsis* Hilliard & Burtt. This growth form seems to have arisen independently at least four times, judging from lack of correlation

with other characters. *Hesperantha humilis* does appear closely allied to two other species with these features, *H. hantamensis* and *H. flava*, but it does not seem worthwhile to recognize this alliance in a formal taxonomic way because this overemphasizes the significance of these characters and obscures their close relationship with several caulescent species of the western Karoo.

There is little else of broad taxonomic importance in the vegetative characters. Unusual leaf modifications occur in a few species, e.g. thickened margins in *H. fibrosa* Baker, pubescence in *H. pilosa* (L. f.) Ker, terete form in *H. juncea* Goldbl. ined., but none of these characteristics are of more than specific significance. Often one leaf is modified to sheath the lower part of the stem, while a second one may become bract-like and without a free apex. These trends seem to be repeated in several lines, and do not appear to constitute a character of much value above species level.

FLOWER AND FLORAL BRACTS

Floral variation in *Hesperantha* is fairly limited. All but a few species have similar, small, actinomorphic flowers, with moderately long, straight perianth tubes and subequal, spreading tepals. White to cream colored flowers predominate in the genus, but pink is the most common color in species in eastern southern Africa and the tropics (B. L. Burtt, pers. comm.). White and cream flowers are evening blooming, and brightly colored ones generally day blooming. In the winter rainfall area there are species with pink, purple, blue, or yellow and often large flowers and these seem to have evolved repeatedly from ancestors with small white flowers. Thus flower color appears to have limited taxonomic value.

A curved perianth tube is present in several species: notably in *Hesperantha radiata* and its relatives; in *H. bachmannii* and *H. bulbifera*; and in *H. grandiflora*. Judging from associated morphological features, these three groups are unrelated. *Hesperantha grandiflora* seems unique in having truly declinate stamens and is zygomorphic. In other species with a curved perianth tube the stamens tend to fall together as they hang downward, thus appearing more or less unilateral. The stamens are included in the perianth tube in the two unrelated species *H. elsiae* Goldbl. ined. and *H. cedarmontana* Goldbl. ined.

Floral bracts are always herbaceous, usually of moderate size, and about as long as the perianth tube. The bracts are noticeably well developed in the very long-tubed species such as *Hesperantha grandiflora*, *H. huttonii*, and some other eastern species and also in the acaulescent species of the western Karoo like *H. humilis*, *H. flava*, and *H. luticola*. The outer bracts of *H. radiata* and its allies are distinctive in having a lower tubular portion encircling the stem, sometimes for as much as two-thirds of their length (*H. radiata*) but barely so in *H. marlothii*, which nevertheless seems allied to the group. These unusual bracts seem to unite a group of species that have other shared features such as curved perianth tubes and characteristically short narrow leaves. This apparently natural alliance includes the widely distributed *H. radiata–H. tysonii* complex and several local southwestern Cape endemics, as well as the Transvaal–Zimbabwe–Malawi *H. longicollis*. It seems useful to give taxonomic recognition here to the alliance, all species of which have imbricate corm tunics.

CYTOLOGY

Basic chromosome number in *Hesperantha* is $x = 13$ (Goldblatt, 1971, and in prep.). Some 25 species have so far been counted, covering the entire range of the genus, and no variation in numbers has been found, except for the presence of B chromosomes in *H. luticola*.

SUBGENERIC CLASSIFICATION

I have decided on sectional rank for each major infrageneric grouping even though the concentric versus imbricate tunic type seems of more fundamental significance than the subtypes of imbricate tunic (and hence perhaps deserving of higher ranking). This is because of the difficulty in assigning certain species to tunic type (owing to distortion by accumulation of old tunics, to soil conditions, or to apparent intermediacy of the corm for this character).

Although corm morphology has been emphasized, all features of the plant have been taken into consideration. The following infrageneric system is proposed. Those species with concentric corm tunics are assigned to what may be considered the least specialized section, *Concentrica*. Species with imbricate tunics have been divided among three sections. Section *Imbricata* includes species with more or less globose, asymmetric corms and bracts with free margins.

Species with bracts having margins partly united around the stem seem to form a natural alliance and are assigned to section *Radiata*. The corm tunics vary in this section (Fig. 2A–D), but the globose corm with tunics notched below is seen as basic here, with symmetric, flat-sided corms being derived.

A fourth section, *Hesperantha*, appears to constitute a natural alliance amongst the species with imbricate corm tunics and is characterized by having symmetric, flat-sided corms, campanulate to triangular in outline. This corm type is a modification of the asymmetric corm of section *Imbricata*, in which the small flattened area at one end of the corm has become enlarged into a conspicuous broad flat side.

HISTORICAL NOTE

The only significant systematic treatments of *Hesperantha* that deal with substantial numbers of species are Baker's revisions in *Handbook of the Irideae* (1892) and in *Flora Capensis* (1896). In neither study was any subgeneric classification established. The main key characters were presence of a straight or curved perianth tube and flower and leaf size. These characters separated species adequately but did not establish any natural groupings. Foster (1948), the only other systematist to have worked extensively on the genus, produced a preliminary study of *Hesperantha* that included corrections to nomenclature and many new species, but this work was not by any means a revision, and no infrageneric classification was presented. Thus the system presented here is essentially new and not founded on any earlier study.

TAXONOMIC TREATMENT

1. **Hesperantha** sect. **Concentrica** Goldbl. sect. nov. TYPE: *H. pilosa* (Thunb.) Ker.

Cormus globosus, ± symmetricus vel asymmetricus, infra ± complanatus, tunicis concentricis, saepe supra subspinosis, floribus actinomorphis vel zygomorphis, albis, rubrescentibus in reversis tepalae exterioris, vel caeruleis, carneis, purpureis, raro flavis, tubo usitato bracteae aequali, in aliquot speciebus perlongo.

Corm ± symmetric to asymmetric, with one side flattened below, the flat side often extending downward for some distance, tunics concentric, outer layers completely enclosing inner, fragmenting irregularly into unequal sections, often drawn into points above. Flowers actinomorphic rarely zygomorphic, whitish, blue, pink, or purple, occasionally yellow, often small, tube well extended from bracts in a few species. Leaves pilose in *H. pilosa* or ciliate in *H. ciliolata*, margins thickened in *H. fibrosa* and occasionally in *H. pilosa* and other species.

Distribution: widespread, southwest Cape to Ethiopia and Cameroon.

Type species: *H. pilosa* (Thunb.) Ker Species: ca. 25

Section *Concentrica* comprising about 25 species, is the largest and most widespread section, ranging from the southwestern Cape to Ethiopia and Cameroon. It has radiated extensively in the southern African Drakensberg, and in the southwestern Cape and western Karoo where some 11 species occur. An evolutionary trend is evident in the reduction in number of leaves to three, one of which partly sheaths the stem. A specialized bract leaf is present on the stems of several species, this sometimes membranous and scale-like. *Hesperantha pilosa* is the only pubescent species in the genus, and *H. ciliolata* is the only one with ciliate leaves. Unusual corm tunics occur in *H. fibrosa* in which the upper part of the tunic is drawn into very long, persistent fibers. In several Drakensberg species and the tropical African *H. alpina* the tunic layers may be papery in texture, rather than brittle and woody. A similar condition is present in *H. montigena* of the SW Cape Mts.

2. Hesperantha sect. **Imbricata** Goldbl. sect. nov. TYPE: *H. humilis* Baker.

Cormus asymmetricus, ± globosus, tunicis imbricatis, infra in segmentis aequalibus incisis, floribus actinomorphis, albis, carneis, luteis, raro maculis atrocoloris, tubo perianthii recto vel curvato in *H. bachmannii* et *H. bulbifera*, habitu caulescenti vel acaulescenti.

Corm ± asymmetric, with one side flattened, and sometimes extending downward for a short distance, imbricate, outer layers overlapping inner above only, usually fragmenting regularly below into even-sized sections, sometimes drawn into points above. Flowers actinomorphic, white, pink, purple, yellow, sometimes with dark contrasting markings, small to large, tube well exserted from bracts in several species, perianth tube curved in *H. bachmannii* Baker and *H. bulbifera* Baker. Plants caulescent or acaulescent, and then with large bracts.

Distribution: centered in western Southern Africa, mainly in arid areas. Namaqualand to Transvaal.

Type species: H. humilis Baker Species: 12

Section *Imbricata*, comprising some 12 species, is centered in the western Karoo, but in fact extends from northern Namaqualand through the Karoo to the Transvaal. The acaulescent habit is developed in three species, *H. humilis* and *H. hantamensis* of the western Karoo, and *H. flava*, which is known from northern Namaqualand and the Laingsburg district of the Karoo. Two species have a

curved perianth tube, the widespread *H. bachmannii*, and *H. bulbifera*, which occurs in the eastern Cape and at isolated montane sites in the Transvaal. Local endemics include the long-tubed *H. pallescens* Goldbl. ined. from the western Cape and *H. oligantha* Diels and *H. purpurea* Goldbl. ined. from the Calvinia district. The most striking species is *H. vaginata*, which has deep yellow flowers with contrasting dark brown markings.

3. Hesperantha sect. **Radiata** Goldbl. sect. nov. TYPE: *H. radiata* (Jacq.) Ker.

Cormus ± globosus et asymmetricus, vel campanulatus et symmetricus, tunicis infra serratis spinosis vel ciliatis, vel in segmentis aequalibus incisis, marginibus bractearum in parte inferioribus connatis vel ± libris, floribus ± actinomorphis sed tubo perianthii curvato, usitatis pallidis, vel carneis.

Corm either ± asymmetric with one side flattened below or symmetric and campanulate in outline, tunics imbricate, outer covering inner only above, unbroken, or notched regularly below into sections, these sometimes ± ciliate-edged, occasionally lower margins of layers serrate to spiny. Outer bract margins usually united below around the axis, sometimes for over half their length. Flowers ± actinomorphic, but usually with curved perianth tube (straight in *H. juncifolia* Goldbl. ined. and barely curved in *H. brevifolia* Goldbl. ined.) and pendulous, unilateral anthers, white-cream, or pale to deep pink, tube well exerted from bracts in some species.

Distribution: widespread in southern Africa, Namaqualand to Malawi.

Type species: *H. radiata* (Jacq.) Ker Species: 7–9

Section *Radiata* comprises a close knit group of seven to nine species centered around the *H. radiata–H. tysonii* complex. This complex extends from Namaqualand through the southwestern Cape and Karoo into eastern southern Africa as far as Swaziland. Corm tunics vary to an unusual extent even within *H. radiata* sensu stricto, but the characteristic bracts usually with united margins and several, small leaves unite the section. There are several local endemics in the southwestern Cape including the terete-leafed *H. juncifolia* from Bredasdorp coast and *H. elsiae* from the Cedarberg, which has included stamens and style branches. *Hesperantha marlothii*, centered in the Roggeveld, has flat-sided corms with spiny margins and it, as well the SW Cape *H. brevifolia* have bracts in which the margins are barely fused. Section *Radiata* extends into Botswana, Zimbabwe, and Malawi where the long tubed *H. longicollis* Baker occurs in wet sites on the highveld and in mountain areas. *Hesperantha ballii* Wild is a dwarf species of the Chimanimani Mts. of the Zimbabwe–Mozambique border.

4. Hesperantha sect. **Hesperantha**. TYPE: *H. falcata* (L. f.) Ker.

Corm ± symmetric, with a flat base, campanulate to triangular in outline, tunics imbricate, outer covering inner above only, lower margins entire, or serrate or drawn into spines, sometimes notched below into ± even-sized sections. Flower actinomorphic, usually whitish yellow, or pink to purplish, occasionally with darker markings (in *H. luticola*); tube barely to well exserted from bracts; anthers and style branches included in perianth tube in *H. cedarmontana*. Plants acaulescent in *H. luticola*, and usually so in *H. latifolia*.

Distribution: Restricted to the winter rainfall area, southern Cape to Peninsula and north to Richtersveld.

Type species: *H. falcata* (L.f.) Ker Species: 7

Section *Hesperantha*, comprising some seven species, is restricted to the winter rainfall areas of the southwestern Cape, Namaqualand, and the western Karoo. All species have flat-sided, campanulate, to triangular corms often with toothed or spiny margins. Two species, *H. latifolia* and *H. luticola*, are acaulescent and grow in seasonally moist sites such as rock pools and stream edges. Both have long perianth tubes. Other species have fairly small, relatively short-tubed flowers but *H. cedarmontana* is unusual in having included stamens and the very short style and style branches enclosed in the perianth tube. *Hesperantha spicata* and the very localized *H. saldanhae* Goldbl. ined. have an unusually large number of very small flowers per spike. *Hesperantha spicata* subsp. *spicata* often has leaves with undulate margins, while subsp. *fistulosa* has hollow, terete leaves. *Hesperantha falcata* is the only widespread species, and is very variable. Its flowers may be white or occasionally yellow or cream.

LITERATURE CITED

BAKER, J. G. 1892. Handbook of the Irideae. George Bell, London.

———. 1896. Irideae. *In* W. T. Thiselton-Dyer (editor), Flora Capensis. vol. 6. Reeve & Co., London.

DAHLGREN, R. M. T. & H. T. CLIFFORD. 1982. The Monocotyledons: A Comparative Study. Academic Press, London.

DE VOS, M. P. 1977. Knol ontwikkening by sommige genera van die Iridaceae en die systematiese posisie. Tyds. Natuurwetensk. 17:9–19.

FOSTER, R. C. 1941. Studies in the Iridaceae II. A revision of *Geissorhiza* Ker-Gawl. Contr. Gray Herb. 135:3–78.

———. 1948. Studies in the Iridaceae V. Some new or noteworthy species of *Hesperantha*. Contr. Gray Herb. 166:3–27.

GOLDBLATT, P. 1971. Cytological and morphological studies in the southern African Iridaceae. J. S. African Bot. 37:317–460.

———. 1976. The genus *Moraea* in the winter rainfall region of southern Africa. Ann. Missouri Bot. Gard. 63:657–780.

HILLIARD, O. M. & B. L. BURTT. 1979. Notes on some plants of southern Africa, chiefly from Natal: VIII. Notes Roy. Bot. Gard. Edinburgh 37:285–325.

LEWIS, G. T. 1954. Some aspects of the morphology, phylogeny and taxonomy of the South African Iridaceae. Ann. S. African Mus. 40:15–113.